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is to be noted, also, that Nature seems to have followed in practice the theory by which we have explained her curious development of series. For example, a short willow branch seems to exemplify the $1/3$ phyllotaxy, but a longer stem plainly shows a $\frac{2}{5}$ arrangement. The plum and apple, similarly, are promoted by the careful student from the $\frac{}{5}$ class to the $3/8$ class; and the walnut and butternut, which we are at first tempted to consider examples of the $3/8$ spiral, belong at least to the $\frac{5}{13}$ series, and the suspicion grows on us that, if we could find a perfect branch with a large number of leaves on it, we might ascend still higher in the range of spiral series. But it is of analytical value to be able to assign a plant to a place in one of two series, just as it is helpful to be able to say, " such a leaf has from five to seven pairs of leaflets."

The tulip tree, oaks, hickories, staghorn sumach and alternate leaved dogwood (the last two being arborescent) have the $\frac{2}{5}$ arrangement quite distinctly. In other instances the results were so conflicting, or the practical difficulties of obtaining good specimens were so great, that the summer closed before I could reach definite conclusions, if, indeed, it is possible to ascribe plants to certain series in all instances.

With the exception of the dogwoods, variations in phyllotaxy never cross generic lines and seldom if ever infringe upon the limits of families.

Reinke's Discussions of Lichenology.

By Albert Schneider.

It is thought advisable to give a review of Reinke's paper on lichenology, because this author is doubtless the most competent advocate of modern scientific lichenology. Although much of the author's discussion is based upon theory and the observations of others, yet the papers are of inestimable value to the special student, and we hope that they will be collected and issued in book form. Meanwhile it is hoped that this review may be found useful by those English-speaking students who can not readily avail themselves of the original communications.

I.

THE PODETIUM OF CLADONIA.*

This paper is in reality a criticism of Krabbe's† monograph of the genus *Cladonia.* Krabbe maintains that the podetia belong to and are a part of the spore-bearing organs (apothecia). His conclusions are based upon the observation of the morphological characters and the mode of development which, according to Reinke and other modern biologists, are not sufficient. Nor can the morphological characters or structure be deduced from its development. Krabbe assumes that since the podetia of *Cladonia* originate in a manner similar to the apothecia of *Ramalina, Parmelia, Lecanora,* etc., they must be apothecial structures. The entire discussion depends upon the points of view. Krabbe, having considered the podetia from the morphological and developmental point of view, naturally comes to different conclusions from Reinke, who views the same structures from the physiological standpoint. It is an excellent example illustrating the necessity of combining morphology and physiology. Reinke very aptly states that if we allow morphology and development to dominate our investigations we may come to the absurd conclusion that the floral leaves are foliage-leaves and, *vice versa,* that the foliage-leaves are floral leaves. Extending the illustration we might conclude that mosses are liverworts, and that fungi are algae, etc. Reinke believes that the development of an organ should be represented as describing a curve which extends from the beginning to the point of maximum development of that organ. All intermediary stages of development are to be considered, but the special importance is to be attached to the fully developed structure. According to this view thallus, foliage-leaf, thorn, tendril, sepal, petal, stamen, pistil, should be represented as terminating at different points of the curve. With these and similar introductory considerations, the author finally enters upon the discussion of the podetia of *Cladonia.*

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* Reinke, J. Abhandlungen über Flechten. I. Das Podetium von *Cladonia.* Pringsheim's Jahrbücher, 26: 495-523. 1894.

† Krabbe, G. Entwickelungsgeschichte und Morphologie der polymorphen Flechtengattung *Cladonia.* Ein Beitrag zur Kenntniss der Ascomyceten. Leipzig (A. Felix). 1891.

Reinke contents himself with de Bary's definition of the lichen-thallus; de Bary designates it as the vegetative organ bearing the apothecia, spermagonia, and in certain instances also pycnidia. This rather negative definition is accepted by most modern lichenologists who define the vegetative organ as the structure whose prime function is to take up and assimilate food-substances. Reinke also accepts, or at least expresses his disinclination to change, de Bary's definition of the reproductive organs; that is, the reproductive organs are the apothecia and spermagonia. If the experiments and observations of Stahl* and Sturgis† prove correct it would be more correct to speak of the *carpogone* and *spermagone* as the reproductive organs; but since it is highly probable that the spermagonia are merely parasitic fungi, or since their true nature is as yet problematical, we have no scientific authority to designate them as reproductive organs. This difference of opinion does not have any important bearing upon the question under consideration. It is, however, evident that Reinke considers the spermagonia as reproductive organs.

Reinke recognizes two portions of the *Cladonia*-thallus: the horizontal portion which is also called primary thallus or protothallus, and the vertical portion, or the podetium of lichenologists. The term thallus is quite generally applied to the horizontal or primary thallus, while the term podetium is retained to designate the vertical thallus. In all instances the podetium takes its origin from the gonidial (algal) zone of the horizontal thallus. Whether the beginnings of the podetium are due to a sexual act or not, is not definitely known. Krabbe and Reinke are inclined to believe that it is nonsexual. Reinke, however, hints at a *possible* sexual act represented by a fusion of the nuclei of two neighboring hyphal cells.

The primary axis of the podetium is negatively geotropic, thus differing essentially from the transversely geotropic dorsiventral horizontal structure of the primary thallus. If the podetia branch, it is found that the negative geotropism decreases with the number of branchings. In cross section the podetium is seen to have a radial structure, hollow, bearing a gonidial zone just within the outermost protective (cortical) covering. The assimilative surface of the podetium is usually much greater than that of the thallus-lobe; from which it took its origin. Both Krabbe and Schwendener * look upon the two distinctive forms of thallus as a species of alternation of generation. Wainio † believes that the apothecial stalk is converted into a vertical thallus by a form of metamorphosis. A similar view is held by Reinke; that is, the podetium was originally an apothecial stalk (perhaps comparable to that of the Caliciaceae and of *Baeomyces*) which finally became metamorphosed into a true thallus. This metamorphosis was of such a nature that the increase in size and assimilative function of the podetium corresponded to a decrease in size and function of the primary thallus.

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* Stahl, E. Beiträge zur Entwickelungsgeschichte der Flechten, I. and II., Leipzig. 1877.

† Sturgis, W. C. On the Carpologic Structure and Development of the Collemaceae and Allied Groups. Proceedings of the American Acad. 25: 1890.

The author enters into a more detailed discussion of the morphological characteristics of the leading types of *Cladonia* for the purpose of illustrating the structural modifications of the podetium and its relation to the primary thallus and apothecia. Life-size figures of the types accompany this discussion. Reinke quite frequently speaks of "fertile forms" when only "pycnidia" are present, which shows conclusively that he considers these structures as reproductive organs coequal in importance to the apothecia. The fact that the pycnidia (and spermagonia) may occur on either the primary thallus or the podetium, while the apothecia occur on the podetia (excepting a few *Cladonias* which are said to have no podetia or only pseudo-podetia) does not seem to raise any question in the author's mind as to the feasibility of considering the former as true sexual organs. This is only in passing, but it is well to remember that sexual organs are generally not so variable in their occurrence and position on the vegetative portion as the pycnidia and spermagonia evidently are.

Without going into further details the following summary may be given of Reinke's reasons for assuming that the podetium is a thallus rather than a reproductive organ.

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* Schwendener, S. Untersuchungen über den Flechtenthallus. Nägeli's Beiträge zur Wissenschaftlichen Botanik, 2: 169. 1860.

† Wainio, Monographia Cladoniarum Universalis. Helsingfors, 1867.

1. A gonidial layer is present whose special function is that of assimilation. This is, however, not conclusive, since all apothecia with a thalloid exciple contain gonidia (algae), and therefore aid in the process of assimilation.

2. The extreme variability in the size and form of the podetium indicates that it belongs to the vegetative portion of the plant rather than the reproductive portion. Constancy in size and form is peculiar to the organs of reproduction.

3. The association of a large primary thallus with a small podetium and, *vice versa*, a small primary thallus (or none at all) with well developed, much-branched podetia seems to indicate that the podetium is specially adapted to supplant the function of the primary thallus.

4. Cladonias with highly developed podetia (*C. furcata*, *C. rangiferina*, etc.) are quite generally sterile (devoid of apothecia) and with primary thallus rudimentary or wanting. It would be absurd to consider such plants as reproductive organs since their prime function is vegetative.

Reinke admits that the podetia are phylogenetically derived from apothecia and thus in part agrees with Krabbe. The following are the main reasons for assuming that this is the case:

1. Podetia are developed endogenously from the gonidial zone of the primary thallus, similar to the apothecia.

2. Podetia have a radial structure similar to apothecia and apothecial stalks. This is in sharp contrast to the dorsiventral structure of the primary thallus.

3. The apothecia occur upon the podetia. An apparent exception is met with in *C. miniata* in which the apothecia seem to be sessile upon the upper surface or margin of the primary thallus. In this case the podetium has become much reduced, while the primary thallus has become much enlarged.

The general conclusion at which Reinke arrives is that *the podetium is a true lichen-thallus phylogenetically derived from the apothecium.*

II.

THE SYSTEMATIC POSITION OF LICHENS.*

This paper is a critical review of lichenology since the time of Schwendener's epoch-making investigations.† The author credits De Bary with first having indicated the dual nature of lichens by demonstrating that species of *Nostoc* and *Chroococcus* may be converted into gelatinous lichens upon becoming penetrated with the hyphae of certain parasitic Ascomycetes. It must be remembered that as late as 1863 Schwendener still believed that the gonidia (algae) were developed upon lateral and terminal branches of the hyphae.‡ De Bary made his discovery in 1865. In 1868§ Schwendener accepted this view and added that all lichens were the result of the union of an alga with some fungus. As the result of his investigations Schwendener concludes that lichens should no longer be considered as a distinct class, but as fungi parasitic upon algae (gonidia). He states: "In development the vegetative organs and the organs of reproduction of lichens are in all respects similar to those of *Ascomycetes*." Reinke has always agreed with Schwendener in the belief that the gonidia of lichens were true algae and the hyphae true fungi. Their opinions differed, however, as to the relationship of the two organisms. Reinke was not at all willing to look upon it as a form of ordinary parasitism. During the summer of 1872, in verbal communication with Griesebach, Reinke pointed out that the relationship indicated a mutual benefit. While the alga supplied the fungus with assimilated food-substances, the latter supplied the alga with water, nitrogen, phosphorus, sulphur and mineral salts. The relation of the fungus and alga in the lichen was comparable to the relation of the root and the leaves of a tree. In order to distinguish this form of relationship (symbiosis) from parasitism (antagonistic symbiosis) it was necessary to introduce a new term. Reinke and Grisebach finally hit upon the word "consortism" as being especially appropriate. Reinke gives conclusive evidence that he has not been duly credited with first having pointed out the true conditions met with in the lichen thallus. This credit is given to de Bary, who is generally supposed to have been the first to point out and explain the phenomenon of "symbiosis" * as it occurs in lichens. The author had, however, previously explained this condition in three different publications.† From these it is evident that De Bary was not the discoverer of the phenomenon now known as mutualistic symbiosis, and that the term consortism antedates that of symbiosis. Reinke explains his views with regard to the lichen-thallus more fully as follows: "We have, therefore, in the thallus of lichens, a consortism, the components of which form a unit, a morphological individual, somewhat as the different tissues in a higher plant unite to form the individual. The fact that the alga can exist independently is dependent upon its ability to assimulate carbon. In the state of consortism, at least in the heteromerous thallus, the alga is nourished by the enclosing fungus; that is it receives from the hyphae the necessary minerals, nitrogen, oxygen, hydrogen and water. The alga in return supplies the fungus with the essential carbon compounds. From this it is evident that the components (alga and fungus) are biologically associated, mutually dependent upon each other, for the formation of the organic substances required for the upbuilding of the common body." The above is certainly conclusive evidence that Reinke had a correct view of the mutualistic relationship of alga and fungus in the lichen-thallus and furthermore that he was convinced that the lichen formed an autonomous structure.

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* Reinke, J. Die Stellung der Flechten im Pflanzensystem. Pringsheim's Jahrbücher, 26: 524–542. 1894.

† Schwendener, S. Die Algentypen der Flechten-gonidien. Basel, 1869.

‡ Schwendener, S. Nägeli's Beiträge zur Wissenschaftlichen Botanik, 3: 133–136. 1863.

§ Schwendener, S. Nägeli's Beiträge zur Wissenschaftlichen Botanik, 4: 195–202. 1868.

The author expresses it as his opinion that the fungi of the higher Ascolichenes no longer exist independently, perhaps never so existed. The alga is, however, still able to lead an independent existence. It is also evident that there are free algae closely related, if not identical with the gonidia of lichens. This fact is of great importance in the consideration of the phylogenetic devel-

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* De Bary, Die Erscheinung der Symbiose. Strassburg, 1879.

† Reinke, J. Göttinger Nachrichten. p. 100. 1872.

Reinke, J. Morphologische Abhandlungen. Leipzig, 1873.

Reinke and Grisebach, A. S. Oersted's System der Pilze, Lichenen und Algen. 1873.

opment of lichens. It is practically impossible to determine what free fungi are identical with the fungi of lichens. All investigators in this line have met with very unsatisfactory results, a thing naturally to be expected. According to Tavel* the fungi of the Collemaceae, Arthoniae and Lecideaceae are more or less closely related to the Patellariaceae. The relationship of the fungi of the Pertusariae, Lecanareae, Pannarieae, Umbilicarieae, Peltidiaceae, Parmeliaceae, Usneaceae, Cladoniaceae, Sphaerophoreae, Ephebeae and Lichineae is practically unknown. The Verrucarieae, Decampieae and Endocarpieae are related to the Amphisphaeriae, Sphaerelloideae. Such uncertainty is certainly very unsatisfactory

Although there may be algae, such as *Cystococcus humicola*, *Pleurococcus vulgaris*, *Nostoc lichenoides*, etc., which only await the opportunity to unite with some fungus to form a lichen, yet it is evident that no true Ascomycete has the power to enter into such a union. There is great uncertainty as to the exact method by which the first lichen or lichens were formed. The author makes the following hypothetical assumption: " In the beginning several lichens were formed by the union of true fungi with algae. According to Möller† such a process is now going on in the case of *Cora pavonia* and the related forms of *Dictyonema* and *Laudatea* The gelatinous lichens are very likely the oldest forms of the Ascolichenes. Such a gelatinous lichen took its origin as the result of the parasitic union of a fungus and a spherical colony of *Nostoc lichenoides.* The question of the origin of the fungus coincides with the question of the phylogenetic origin of parasitic fungi in general and need not be further discussed. The fungus which at first behaved like a true parasite (antagonistic symbiosis) took its entire food-supply from the nostoc. The condition of mutualism (consartism) was a phylogenetic product; perhaps due to natural selection or other formative causes resulting from the union of alga and fungus. From this proto-*Collema* other gelatinous lichens were evolved; finally also such with heteromerous thallus. It is probable that in the course of phylogenetic processes the developing spores of gelatinous lichens acquired the ability to enter into a mutually symbiotic union with other algae. A series phylogenetically derived from *Collema* may have taken an upward course, that is, proceeded from the lower to the higher, from the simpler to the more complex. As an example we may cite the natural series *Collema*, *Leptogium*, *Hydrothyria*, *Peltigera*. If *Stictina* is derived from *Peltigera*, *Sticta*, which is evidently *Stictina* with bright green algae, would also be included in the series. Every phylogenetically derived lichen-type constituted the beginning of a new series which may have proceeded upward or downward; that is in the direction of either higher or lower forms. In certain cases it is difficult to decide whether given lichens form the beginnings of a series or whether they are degenerate forms. Among such doubtful forms are included *Biatora uliginosa*, *Thelidium minutulum*, and species of *Buellia* and *Arthonia*. Many of these plants live parasitically upon other lichens, and no doubt bear a relation to these similar to the relation of *Cuscuta* and *Monotropa* to the chlorophyll-bearing genera of the same family. The above summary leads to the conclusion that there is a natural system of lichens distinct from that of fungi.

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*Tavel, F. Vergleichende Morphologie der Pilze, pp. 94 and 108. Jena, 1892.

† Möller, A. Ueber die eine Thelephoree, welche die Hymenolichenen: *Cora Dictyonema* und *Laudatea* bildet. Flora 77: 254–278. 1893.

The author deplores the pernicious effect of Schwendener's plan of the arrangement of lichens. As a result lichens received only casual mention in an appendix to the different groups of lichens. Lichenologists (systematic) in general have strongly opposed Schwendener's plan of classification. Although Reinke has always sympathized with these lichenologists, yet he regrets very much that they should have made their special attack upon Schwendener's theory of the dual nature of lichens.

The following is a brief summary of the leading items discussed in this paper:

1. The true relation of fungus and alga in the lichen-thallus was first pointed out by Reinke.
2. The term *Consortism* antedates the term *Symbiosis*.
3. Schwendener's (De Bary's) theory of the dual nature of lichens is fully accepted.
4. Most of the algal types occurring in lichens have been specifically determined. The fungal types no longer exist (at least in most cases) and can therefore not be determined.

5. A lichen is a phylogenetically derived morphological unit.

6. Lichens form groups of natural series phylogenetically derived from distinct prototypes. Lichens have, therefore a polyphyletic origin.

7. Lichens differ from the fungi morphologically as well as physiologically.

The following are the general conclusions at which Reinke arrives:

1. Although fully accepting Schwendener's theory, lichens are phylogenetically, morphologically and physiologically wholly distinct from fungi, and it is therefore inconsistent to arrange them under fungi.

2. Lichens form a natural group coequal in systematic importance with fungi and algae.

Since Reinke has written this paper Schwendener in a personal interview with E. L. Gregory [*] stated that he had no objection to the proposed plan of classification. Tubeuf, [†] as well as other recent authors, expresses the opinion that the lichen is an autonomous structure, a morphological unit. There are also strong objections, such as those cited by Lindau. [‡]

A new Gymnogramme from Venezuela, with Remarks on some other Venezuelan Ferns.

By B. D. Gilbert.

Last spring Dr. H. H. Rusby, Secretary of this club, and Mr. R. W. Squires, of Minneapolis, made a botanical trip to Venezuela together and brought back with them a large collection of pressed plants, among which were about two dozen species of ferns. This fall Dr. Rusby placed the ferns in my hands for identification and it is found that although the collection is small it con-

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[*] Gregory, E. L. Notes on the Classification of Lichens. Bull. Tor. Bot. Club. 23: 361. 1896.

[†] Tubeuf, K. F. Pflanzenkrankheiten. p. 102. Berlin. 1895.

[‡] Lindau, G. Die Beziehung der Flechten zu den Pilzen. Hedwigia, 34: 195–204. 1895.